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## NEW MIOCENE MONACHINAE FROM THE WESTERN SHORE OF THE CHESAPEAKE BAY (MARYLAND, USA)

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**New Miocene Monachinae from the Western Shore of the Chesapeake Bay (Maryland, USA).** Rahmat, S. J., Koretsky, I. A., Osborne, J. E., Alford, A. A. — The Family Phocidae includes four subfamilies (Phocinae, Monachinae, Cystophorinae, and Devinophocinae) consisting of medium- to large-sized mammals that possess distinctive adaptations to semi-aquatic life. In the Miocene of the Chesapeake Group, only two subfamilies of the Family Phocidae were identified: Phocinae and Monachinae. *Leptophoca*, a representative of the subfamily Phocinae, appears on the eastern shore of the North Atlantic around 16 million years ago. Recently, two new monachine species, the larger *Terranectes magnus* (n. gen., n. sp.) and the medium-sized *T. parvus* (n. sp.), were recorded in the Upper Miocene of the Chesapeake Group in the Eastover Formation (7.0–6.0 Ma) and St. Marys Formation (10.0–8.0 Ma). These two distinct subfamilies of seals indicate a well-marked divergence between phocines and monachines, much earlier than 18 million years ago, as previously suggested. The Eastover Formation was deposited in a shallow embayment that covered southern Maryland, the coastal plain of Virginia, and the northeastern corner of North Carolina. The geologically older St. Marys Formation represents a tide-influenced coastal environment, with low-salinity estuaries. There was a sharp temperature decrease in the Late Miocene, indicated by a shift to a cooler-water fish fauna during St. Marys time. The Eastover Formation reflects warmer waters with relatively strong currents, significant shoals, barriers, and varied depths.

Fossil evidence of earlier seals suggests that phocids originated in the North Atlantic and otarioids in the North Pacific. True seals diverged from ancient Carnivora in the early Oligocene (or earlier) in the Paratethyan / Mediterranean Basins, spread widely during the Middle Miocene and crossed westward across the Atlantic Ocean, before dispersing in the eastern United States by the Early Pliocene.

Key words: Phocidae, Monachinae, Middle / Late Miocene, Maryland, Calvert Cliffs.

### Introduction

The Family Phocidae (= true seals) includes three extant subfamilies (Phocinae, Monachinae, Cystophorinae) and one extinct subfamily (Devinophocinae) of marine mammals that are morphologically distinct from terrestrial carnivorans with their adaptations to a semi-aquatic life. These four subfamilies should be considered as separate phylogenetic branches (Koretsky and Rahmat, 2015: fig. 8) of early Phocidae, which separated from ancient Carnivora probably in the early Oligocene (or perhaps even before that time) in the Paratethyan / Mediterranean Basins (Koretsky and Sanders, 2002; Koretsky and Domning, 2014; Koretsky and Rahmat, 2015; Rahmat and Koretsky, 2016). Phocids greatly expanded their range during the Middle Miocene in the Paratethyan region, crossed the Atlantic Ocean westward, but then practically ceased to exist in Eastern Europe by the Early Pliocene (fig. 1). These fossil animals were members of the subfamilies to which modern seals belong. The best fossil record of phocid pinnipeds in the USA is from the North Atlantic coast-line, predominantly from the Yorktown Formation (5.2–3.4 Ma) of the Lee Creek Phosphate Mine of North Carolina (Koretsky and Ray, 2008). So far, only two subfamilies of phocid seals (Phocinae and Monachinae) are represented in Neogene deposits of the coastal plain of the eastern United States.

Members of the Family Phocidae do not appear in the North Pacific until either Late Pliocene time (Barnes and Mitchell, 1975), or even more recently (Middle Pleistocene according to Boessenecker, 2013), and their evolutionary history is separate from that of the Otariidae (= sea lions) at least since Late Oligocene time (Koretsky and Barnes, 2006). So, the paleozoogeography of “Pinnipeds” indicates that the Otariidae developed in the North Pacific and the Phocidae in the North Atlantic, with their early geographic divisions due to separate origins. Additionally, the fossil record from the Paratethyan Region agrees with earlier conclusions (Repenning and Ray, 1977; Ray, 1977; Muizon, 1981 a–c, 1982; Koretsky and Rahmat, 2013) that early phocid evolution was primarily in the Atlantic Basin, including Tethys, with the earliest occurrence and greatest diversity of mid-Tertiary fossil phocids known from the Atlantic and Tethyan areas. The close relationships of Miocene and Pliocene seal faunas on both sides of the North Atlantic (Koretsky and Ray, 2008; Koretsky et al., 2012) indicate relatively easy interchange, likely with cross-Atlantic distribution of a large number of species. The Messinian climatic deterioration could have restricted phocids to Southern and Northern latitudes, causing monachines to be pushed southward by cold-loving phocines dispersing from the north (Walsh and Naish, 2002; Koretsky and Barnes, 2006). This would explain the spread of monachine seals on the east coast of North America based on open availability of habitat.

From Miocene fossil remains found on the western shore of the Chesapeake Bay, two subfamilies of the Family Phocidae were identified: Phocinae and Monachinae. *Leptophoca*, a representative of the smaller-sized seals of the subfamily Phocinae, appears on the eastern shore of the North Atlantic first. The occurrence of *Leptophoca* on both sides of the Atlantic Ocean, in The Netherlands and Maryland and Virginia (USA), supports geological and morphological evidence, and shows that *Leptophoca amphiatlantica* (Koretsky et al., 2012) originated in Western Europe (Holland, 16.4–15.8 Ma), crossed the Atlantic Ocean, and settled on the western shore of the North Atlantic (fig. 1), first during deposition of the Calvert Formation (20.0–14.2 Ma), and later spreading southward during the time of the St. Marys Formation (10.0–8.0 Ma). Fossil evidence of the geologically older *L. amphiatlantica* from Europe and the geologically younger *L. lenis* from USA contradicts the reclassification of *Leptophoca* and *Prophoca* by Dewaele et al. (2017).

*Leptophoca lenis* (Phocinae) from the Calvert Formation (~18 Ma), renamed *Leptophoca proxima* by Dewaele et al. (2017), is one of the most primitive representatives of true seals, is widely known to researchers, and has been collected at numerous locations along the western shore of the Chesapeake Bay (fig. 2). Recently, an abundance of fossil material of this species has been collected (deposited primarily in the USNM and CMM), which is very unusual for any fossil seal taxon. However, it is clear that more than one taxon of phocids are present in the Chesapeake Group based on multiple isolated mandibles, postcranial bones and fragmentary skulls.

To date, only a limited number of fossil seal skulls have been described due to their fragility and lack of preservation over time. Thus, fossil seal classification is based primarily on the morphology of fragmentary and dissociated postcranial bones, mainly the humerus and femur. On the contrary, the osteological classification of modern seals is mainly based on cranial material. By examining the ecological niches of modern seals, which are reflected in their morphology, Koretsky’s (2001) ecomorphotype analysis correlates postcranial bones (commonly the humerus and femur) with the mandible into one specific taxon. So, modern seals are able to be separated into ecomorphological units and fossil seals can be placed into analogous ecomorphological groups also. This inferred association of isolated bones (cranial and postcranial) has been confirmed by the finding of an almost complete skeleton of *Monachopsis pontica* (Goldin and Pilipenko, 2012) and has been supported by the finding of isolated elements by others (Cozzuol, 2001; Amson and Muizon, 2014; Berta et al., 2015).

Overall, the study of extinct seals in the Western Paratethys (Western Europe) was severely limited by the scarcity of fossil finds, contrary to the numerous specimens known from the United States. Recently, the finding of two new extinct monachines was recorded in the Upper to Middle Miocene of the Chesapeake Group in the Eastover Formation (7.0–6.0 Ma) and St. Marys Formation (10.0–8.0 Ma). The discovery of *Afrophoca libyca* (Koretsky and Domning, 2014), one of the oldest monachine seals, and the previous description of one of the oldest phocine seals (*Leptophoca amphiatlantica*, Koretsky et al., 2012), demonstrate a well-marked divergence between phocines and monachines much earlier than 18 million years ago, as previously suggested (according to Árnason et al., 2006).

**Abbreviations** — specimens from the following institutions and departments have been examined for this manuscript:

**CMM-V**, Calvert Marine Museum, Solomons, Maryland, USA; **MAB**, Museum de GroenePoort (formerly Museum Ammonietenhoeve), Boxtel, The Netherlands; **SAS**, South African Naval Museum, Simon’s Town, South Africa; **UAM**, University of Alaska Museum, Fairbanks, Alaska; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

#### Geology, Stratigraphy and Paleoenvironment of some sites along Calvert Cliffs

A variety of sedimentary conditions are represented in the Calvert Formation, including a predominantly open marine environment with a gently sloping seafloor (~150m water depth), adjacent to a warm-temperature terrestrial flora with some subtropical elements (Gottfried et al., 1994). Some of the fossil seal material was recovered from Bed12, the deepest water facies preserved within the formation, which also includes remains of other marine mammals, fish, reptiles, abundant mollusks, and diverse micro-plankton (Kidwell, 2006). The Calvert record indicates repeated transgression-regression cycles, each having a maximum water depth shallower than that of the previous cycle.

The St. Marys Formation (Beds 22–24) was deposited between approximately 10.0 and 8.0 Ma (fig. 3). Sediments of the St. Marys Formation are medium to coarse sands and pebble beds, with abundant wood and other plant debris and small shells, which represent mixed marine and freshwater conditions in a tide-influenced coastal environment (Kidwell, 2006). Marginal marine environments are less diverse, and include species that are typical of low-salinity estuaries (Barnes et al., 2006). A sharp temperature decrease in the Late Miocene is indicated by a shift to a cooler-water fish fauna during St. Marys time (Gottfried et al., 1994).

All Monachinae specimens described herein were found at Site #PQ-BH9812 (fig. 3) by Jason Osborne and Aaron Alford between September 2011 and September 2012 in southern Southampton County, Virginia, near the North Carolina border. All specimens were found floating within yards of the exposures, with several bones preserving lithified matrix. The site comprises a series of exposures of highly fossiliferous Upper Miocene marine sediments unconformably overlain by unfossiliferous Pleistocene or Holocene sand deposits. Pliocene contamination is unlikely since Pliocene sediments are not visibly present at the site and are not reported in nearby USGS coreholes (Weems et al., 2010).

In the prototypical stratigraphic sequence of southeastern Virginia (fig. 3), the Lower Upper Miocene (Tortonian) St. Marys Formation (Chesapeake Group) underlies the Upper Miocene (Messinian) Eastover Formation (Chesapeake Group; Weems et al., 2010). The Eastover Formation consists of well-sorted clayey sands and silty clays deposited from 7.0 to 6.0 Ma (Powars and Bruce, 1999) in a shallow embayment that covered southern Maryland, the coastal plain of Virginia, and the northeastern corner of North Carolina (Ward and Blackwelder, 1980). Mollusk and ostracod evidence from the USGS Langley (Langley, Virginia) corehole to the east suggests an inner-middle neritic environment periodically influenced by upwellings of cooler water (Edwards et al., 2005).

In southeastern Virginia, deposits of the St. Marys Formation are unconformably overlain by the Upper Miocene Eastover Formation (also Chesapeake Group; Ward and Blackwelder, 1980). Evidence from strontium-isotope dating indicates that the unconformity between the two formations represents very little time (Powars and Bruce, 1999). The Eastover Formation is most easily differentiated from the Pliocene Yorktown Formation by the presence of thick, sandy shell beds dominated by the mollusks *Isognomon*, *Mercenaria* and *Chesapecten*. *Isognomon* is abundant in the Eastover, but does not appear in later formations (Ward and Blackwelder, 1980). Beds of this nature are present at Site #PQ-BH9812 and include dense lenses of the mollusk *Isognomon*. The presence of *Isognomon* near the top of the Miocene exposures indicates that there is little possibility of Pliocene contamination.

The mollusk assemblage indicates that the Eastover Seas were sub-tropical and resembled the depositional conditions currently found near Florida in the Gulf of Mexico (Edwards et al., 2005). Ward and Blackwelder (1980) suggested that the later beds of the Eastover Formation reflect relatively strong currents, significant shoals, barriers, and varied depths, based on differences in relative elevation and composition of outcrops throughout Virginia.

At Site #PQ-BH9812, the Eastover Formation is characterized by two distinct facies. The upper portion of the exposure consists primarily of dense sandy shell beds dominated by the mollusks *Isognomon*, *Mercenaria*, and *Chesapecten*. These facies most likely represent the Cobham Bay Member of the Eastover Formation. This is underlain by sandy beds characterized by blue-gray sands, no visible intact shells, and well-preserved mammalian bone with little or no displacement, distortion or surface wear.

The Eastover Formation may contain as many as four distinct members (Powars and Bruce, 1999; Edwards et al., 2005), though only two have been formally described (Ward and Blackwelder, 1980). In the absence of microfossil evidence, it is impossible to warrant any firm claims as to the member of the Eastover Formation represented by the sandy facies at the base of the outcrops. The physical characteristics of a sample taken near the bottom of the exposure (by A. Alford and J. Osborne) are consistent with fine-grained and only sparsely shelly facies of the Eastover Formation.

In exploring the site, no contact has been found with the underlying St. Marys Formation. Ward and Blackwelder (1980) stated that the contact between the Eastover and St. Marys formations is generally sharp and characterized by pebbles and phosphate nodules. Nearby USGS coreholes confirm this observation locally, though there is some variability in the reported composition of the contact between the two formations (Weems et al., 2010). Exploration of site # PQ-BH9812 has revealed no evidence of the contact with the St. Marys Formation or *in situ* concentrations of pebbles and phosphate nodules. On at least two occasions, however, large quartz pebbles were found *in situ* at the very bottom of the exposures suggesting that the contact with the St. Marys Formation may be not far below the exposure.

#### List of localities

Additional localities where fossil seal material has been found (between the black lines in fig. 2) include, in Maryland: Brownie's Beach (also known as Bayfront Park; Bed 14); Camp Roosevelt (Bed 14); Calvert Beach (Bed 14–16); Chesapeake Beach (Bed 5); Chesapeake Ranch Club (Bed 18); Flag Ponds State Park (Bed 14); Governor's Run (Bed 15); Kaufman Camp (Bed 14); Matoaka Cottages (500 yd. N. of Kings Creek; Bed 17); Randle Cliff (also known as Naval Research Lab; Bed 14); Parker's Creek (Bed 12); Plum Point (Bed 10); Port Republic (also known as Scientists Cliffs; Bed 14); Prince Georges County, Tinker Creek (Bed 17); Scientists' Cliffs (Bed 13); St. Leonard (also known as Calvert Beach; Bed 18); Willow Beach Colony (Bed 8). In Virginia (Calvert and St. Marys formations): Stratford Harbor; Beach Development, VA Potomac Mill Pond, Gravitts Mill, Westmoreland County, Pope's Creek in Stratford; Westmoreland County, Westmoreland State Park (Horsehead Cliffs), Stratford Hall, Nomini Cliffs, Stratford; Hanover County, south bank of Pamunkey River, beach near Mill Wheel.

**SYSTEMATIC PALEONTOLOGY****Class MAMMALIA** Linnaeus, 1758**Order CARNIVORA** Bowdich, 1821**Family PHOCIDAE** Gray, 1825**Subfamily MONACHINAE** Trouessart, 1897***Terranectes* gen. n.**

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Etymology. *Terra* (Latin word for “ground, Earth”) and *nectes* (Greek word for “swimmer”), implying a semi-aquatic animal adapted more for terrestrial movement than aquatic.

Type species. *Terranectes magnus*, **sp. n.**

Included species. In the Upper Miocene of the Chesapeake Group two new monachine species are recorded: *T. magnus* and *T. parvus*.

Diagnosis. Monachine seals of medium to large size. Posterior border of glenoid fossa of skull forms deep, wide postglenoid groove in tympanic bone; postglenoid foramen located at end of postglenoid groove, not floored by tympanic bone; long axis of tympanic bulla parallel to midline of skull; carotid canal parallel to surface of basioccipital, its posterior aperture opens ventrally, medial side has fully formed margin.

Humeral deltoid crest strongly developed, short, terminates at middle of diaphysis (similar to *Piscophoca pacifica* and in contrast to *Acrophoca longirostris*, *Pontophoca sarmatica*, *Callophoca obscura*, *Pliophoca etrusca*); greater width of deltoid crest located on its proximal part (similar to *Pontophoca sarmatica*, *Pliophoca etrusca*; and opposite to both *Pis. pacifica* and *Acr. longirostris*, where entire deltoid crest approximately same width); in lateral view deltoid crest flattened and oval (similar to *Pis. pacifica*, *Pliophoca etrusca*; and opposite from *Acr. longirostris*, where deltoid crest significantly elongated; opposite to *Callophoca obscura*, with flattened and square-shape); proximal end of deltoid crest higher than head (similar to *Pliophoca etrusca*; opposite to both *Pis. pacifica* and *Acr. longirostris*, where they have same height; opposite to *Pontophoca sarmatica*, with lesser trochanter higher than head and deltoid crest; opposite to *Callophoca obscura*, with deltoid crest located below lesser tubercle and below or at same level as head).

Femoral greater trochanter extends proximally slightly higher than head (similar to *Pontophoca sarmatica*; and opposite to *Acr. longirostris*, where greater trochanter extends much higher; opposite to *Callophoca obscura*, with head extending higher than greater trochanter; opposite to *Pliophoca etrusca*, with head at same level as greater trochanter); greater trochanter proximal part wider than distal (similar to *Acr. longirostris*, *Pontophoca sarmatica*, *Callophoca obscura*); trochanteric fossa deep, wide, and open distally, reaching the distal border of head (similar to *Callophoca obscura*; opposite to *Acr. longirostris*, *Pontophoca sarmatica* and *Pliophoca etrusca*); intertrochanteric line disappears at middle of diaphysis (opposite to *Acr. longirostris*, with longer intertrochanteric line; opposite to *Callophoca obscura*, with very short intertrochanteric line; opposite to *Pliophoca etrusca* and *Pontophoca sarmatica*, with undeveloped line); supracondylar fossa shallow, slender, elongated, and located above lateral condyle (similar to *Callophoca obscura*; opposite to *Acr. longirostris*, with deeper and larger supracondylar fossa; opposite to *Pontophoca sarmatica* and *Pliophoca etrusca*, with more horizontally-directed supracondylar fossa); condyles unequal in size (similar to *Acr. longirostris*, *Callophoca obscura*, *Pliophoca etrusca*).

Innominate bone similar to typical monachines, without lateral excavation (same as *Pis. pacifica*, *Acr. longirostris*, *Callophoca obscura*); wide, flattened iliac crest (opposite to *Pis. pacifica*, with rounded and short iliac crest and opposite to *Acr. longirostris*, with rounded iliac crest that is less wider than *Terranectes* and more wider than *Pis. pacifica*; opposite to *Callophoca obscura*, with rounded, thick and wide iliac crest); thick specifically across

acetabulum (similar to *Pis. pacifica* and opposite to *Acr. longirostris*); reduced iliopectineal eminence (opposite to both *Pis. pacifica* and *Acr. longirostris*); and shallow acetabulum (similar to *Callophoca obscura*; opposite to *Pis. pacifica* and *Acr. longirostris*, which are deeper and more conical).

Tibia and fibula fused proximally (Muizon and Hendey, 1980).

## Comparisons

**Humerus.** The proximal part of the humeral deltoid crest in *Terranectes* is located higher than the head and lesser tubercle (opposite to *P. pacifica* and *Acr. longirostris*, where they are at the same level and opposite to *Callophoca obscura*, where the proximal part of the deltoid crest is located lower than the head). *Terranectes* has some characters similar to other Monachinae, such as: the lesser tubercle is oval-shaped (except in *Callophoca*, *Piscophoca* and *Acrophoca*); smaller deltoid tuberosity (except in *Monachus* and *Piscophoca*); greater width of deltoid crest located on its proximal part (opposite to both *Pis. pacifica* and *Acr. longirostris*, where the entire deltoid crest remains about the same width); the deltoid crest is flattened and oval shaped in lateral view (similar to *Pis. pacifica* and different from *Acr. longirostris*, where the deltoid crest is much more elongated); lesser tubercle flattened (except in *Callophoca* and *Acrophoca*); intertubercular groove wide and slightly concave (except in *Monachus*, *Pliophoca*, and *Piscophoca*); and deltoid crest is short, terminating at the middle of the diaphysis (except in *Pontophoca* and *Acrophoca*, where the deltoid crest extends further distally). In addition, *Terranectes* differs distinctly from other genera as follows: 1) from *Monachus* (despite similar size): smaller deltoid tuberosity and wide, slightly concave intertubercular groove; 2) from *Pontophoca*: larger size; cranio-caudally compressed head; 3) from *Callophoca*: smaller size; the proximal part of the humeral deltoid crest is located lower than the head and lesser tubercle; 4) from *Pliophoca* (despite similar size): cranio-caudally compressed head; 5) from *Miophoca*: only mandible is known; 6) from *Homiphoca*: larger size; the deltoid crest terminates abruptly; a smaller deltoid tuberosity; the greater breadth of deltoid crest located on its proximal part; 7) from *Hadrokirus martini*: humerus, femur and innominate bones are not available.

**Femur.** The greater trochanter in the *Terranectes* femur extends proximally slightly higher than the head (similar to *Pontophoca sarmatica*). This characteristic is opposite to: *Acr. longirostris*, where the greater trochanter extends much higher than the head; *Callophoca obscura*, where the head extends higher than greater trochanter; and to *Pliophoca etrusca*, where the greater trochanter and head are at the same level. The proximal part of the *Terranectes* greater trochanter is wider than the distal part (similar to *Acr. longirostris*, *Pontophoca sarmatica*, *Callophoca obscura*). In both *Terranectes* and *Callophoca obscura*, the trochanteric fossa is deep, wide, and opens distally, reaching the distal border of the head (opposite to *Acr. longirostris*, *Pontophoca sarmatica* and *Pliophoca etrusca*). The intertrochanteric line disappears at the middle of the femoral diaphysis in *Terranectes*. This line is undeveloped in *Pliophoca etrusca* and *Pontophoca sarmatica*, much longer in *Acr. longirostris* and very short in *Callophoca obscura*. The supracondylar fossa in *Terranectes* is shallow, slender, elongated, and located above the lateral condyle (similar to *Callophoca obscura*). *Acr. longirostris* has a deeper and larger supracondylar fossa while this fossa in both *Pontophoca sarmatica* and *Pliophoca etrusca* is more horizontally-directed. *Terranectes*, *Acr. longirostris*, *Callophoca obscura* and *Pliophoca etrusca* all have condyles that are unequal in size. *Pontophoca sarmatica* has significant expansion of the distal part of femur, a unique feature for this species.

**Innominate.** The *Terranectes* innominate bones do not have any lateral excavation, a typical monachine feature (also seen in *Pis. pacifica*, *Acr. longirostris* and *Callophoca obscura*). *Pliophoca etrusca* and *Hadrokirus martini* do not have any described innominate bones.

*Terranectes* has a wide and flattened iliac crest, opposite to: 1) *Pis. pacifica* (a rounded and short iliac crest; 2) *Acr. longirostris* (rounded iliac crest that is less wider than *Terranectes* and more wider than *Pis. pacifica*; and 3) *Callophoca obscura* (rounded, thick and wider iliac crest). Iliac spines are very prominent in *Terranectes*, but are not well developed in *Callophoca obscura*. Only the cranial ventral iliac spine in *Acr. longirostris* is well developed. The *Terranectes* and *Pis. pacifica* innominate bones are thick, especially across the acetabulum, while in *Acr. longirostris* it is not as thick. *Terranectes* has a reduced iliopectineal eminence, while it is more prominent in both *Pis. pacifica* and *Acr. longirostris*. The acetabulum is shallow in both *Terranectes* and *Callophoca obscura*, but is deeper and more conical in shape in *Pis. pacifica* and *Acr. longirostris*.

Due to the rarity of fossil material and uncertainty of taxonomic relationships of some members of the subfamily Monachinae, further detailed geological and morphological information about other species will be addressed. While *Acrophoca* Muizon, 1981 a from the Lower Pliocene of Peru, re-dated as Late Miocene by Ehret et al. (2012), is a genus seemingly related to *Terranectes* and similar in size, it differs by having: a slightly wider proximal part of the humeral deltoid crest that ends abruptly and the greater breadth of the deltoid crest located on its proximal part.

Another genus related and similar in size to *Terranectes* is *Piscophoca* Muizon, 1981 a, from the Lower Pliocene of Peru, re-dated as Late Miocene by Ehret et al. (2012), differs by: the greater breadth of the deltoid crest located on its proximal part and a well-expressed musculospiral groove. No femur is available for this species.

*Messiphoca mauretunica* Muizon, 1981 b, from the Late Miocene of Algeria is close to the origin of *Pliophoca* and *Monachus*. Only the distal half of the humerus is preserved, but based on the illustrations, *Terranectes* is larger and has a deltoid crest that ends abruptly in comparison to *Messiphoca*. In addition, the ulnae of *Terranectes* and *Messiphoca* have completely different morphologies (see Muizon, 1981 b: figs 1–3).

*Palmidophoca callirhoe* was named by Ginsburg and Janvier (1975) from the Late Miocene (Tortonian) of the Western Paratethys. It was assigned to Phocidae by Ginsburg and Janvier (1975), to Monachinae by McKenna and Bell (1997) and Ginsburg and Janvier (1999), and to Carnivora by Sepkoski (2002). Only the mandible of this species is known.

*Monotherium delognii*, *M. affine*, and *M. aberratum* are large, medium-, and small-sized primitive monachines, respectively, described by Van Beneden (1876) from the Late

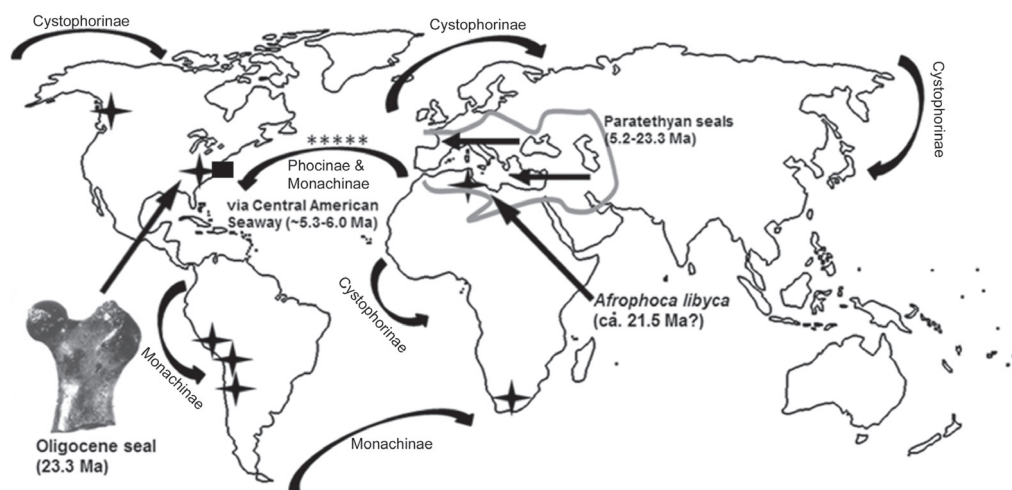


Fig. 1. Phocid dispersal map. World map showing the likely origin of seals in the Paratethyan / Mediterranean basin (gray outline) and their westward dispersal. Both Phocinae (*Leptophoca amphiatlantica*, ~16 Ma) and Monachinae (*Terranectes*, ~ 11 Ma) crossed the Atlantic Ocean and settled on the western shore of the North Atlantic (black arrow with asterisks). The black rectangle indicates the Chesapeake group, the location of the oldest known phocine and monachine extinct seals in North America.

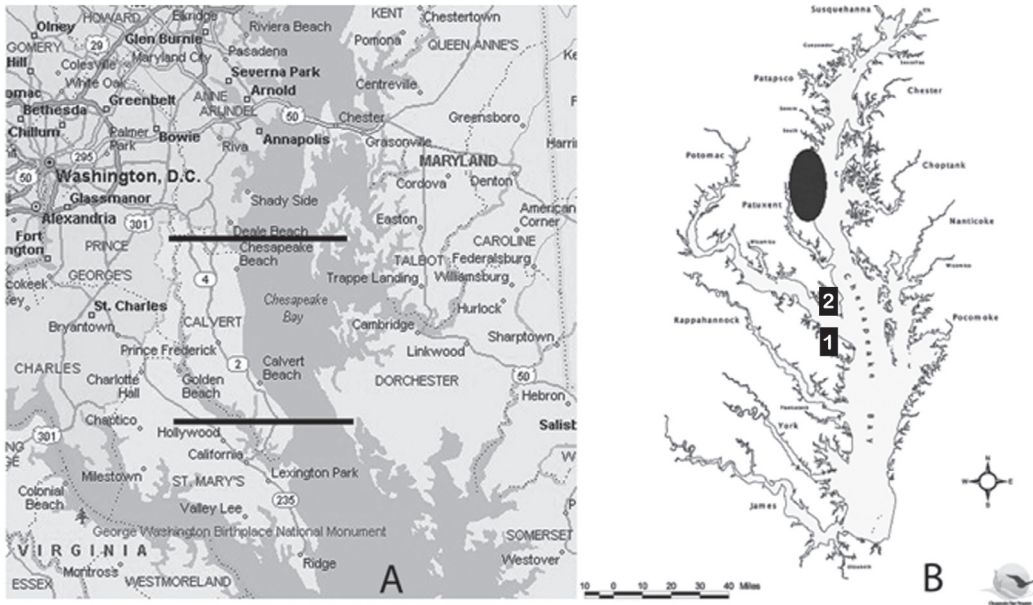


Fig. 2. Chesapeake map. **A** — Chesapeake Bay fossil seal localities in Maryland lie on the west side of the bay between the heavy black horizontal lines (16 locations between Chesapeake Beach and Chesapeake Ranch Estate). **B** — the majority of bones collected between Governor Run and Dares Beach. The number 1 indicates the Eastover Formation (~ 7.0–6.0 Ma; Virginia) and the number 2 indicates the St. Marys Formation (~ 10.0–8.0 Ma; Maryland).

Miocene (Diestian, Borgerhout) of Belgium, but their specific status remains uncertain and the genus requires revision. According to Ray (1976), additional material of *Monotherium* has been collected from the Calvert Formation, and the St. Marys Formation, in eastern North America. However, Ray’s (1976) suggestion to associate these bones to *Monotherium* is seriously questionable and therefore will not be discussed in this paper. The bones of *Terranectes* are larger than *Monotherium* and do not demonstrate any sexually dimorphic features (Koretsky, 2001).

*Prionodelphis rovereti* Frenquelli, 1922, from the Miocene / Early Pliocene of Argentina, is a *nomen dubium*, because, according to Muizon and Henedy (1980), this name was based on two isolated teeth, one of which (the lectotype of the species) belongs to a delphinoid cetacean, whereas the other is a monachine seal tooth with low diagnostic value (Koretsky and Ray, 2008).

Geological age, distribution, and type locality. Upper Miocene, Chesapeake Group, Eastover Formation (7.0–6.0 Ma) and St. Marys Formation (10.0–8.0 Ma), Southampton County, Virginia near the North Carolina border.

PERIOD	EPOCH	AGE	STRATIGRAPHIC UNIT		
NEOGENE (part)	Miocene	upper	10 Ma	Eastover Formation	
				St. Marys Formation	Windmill Point Member
					Little Cove Point Member
		Choptank Formation			
		middle	15 Ma	Calvert Formation	Plum Point Member
					Fairhaven Member
		lower	20 Ma		

Fig. 3. Stratigraphic correlation of the Chesapeake Group. Site #PQ-BH9812, in southern Southampton County, Virginia, near the North Carolina border, exposes beds of the Eastover Formation.

***Terranectes magnus* sp. n.** (figs 4–11; tables 1–5).

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Etymology. *Magnus* (Latin, “big”)

Holotype. CMM-V-4710, proximal half of the left humerus. Collected by J. Osborne and A. Alford, between September 2011 and September 2012.

Type locality. Site # PQ-BH9812, Southampton County, Virginia near the North Carolina border.

Geological age and distribution. Upper Miocene, Chesapeake Group, Eastover Formation (7.0–6.0 Ma) and St. Marys Formation (10.0–8.0 Ma).

Referred specimens. In addition to the holotype, the following specimens were found in southern Virginia near the North Carolina border:

Skull fragment: CMM-V-4680; Atlas: CMM-V-4677; Cervical vertebra: CMM-V-4676; Ulna: CMM-V-4707; Innominata: CMM-V-4704, CMM-V-4705, CMM-V-4708; Femur: CMM-V-4706; Tibia: CMM-V-4702; Thoracic vertebrae: CMM-V-4675, CMM-V-4685; Sacra: CMM-V-4681, CMM-V-4703.

Diagnosis. Seals of large size. Posterior border of glenoid fossa of skull thicker than anterior; postglenoid foramen located at end of postglenoid groove; shallow, wide

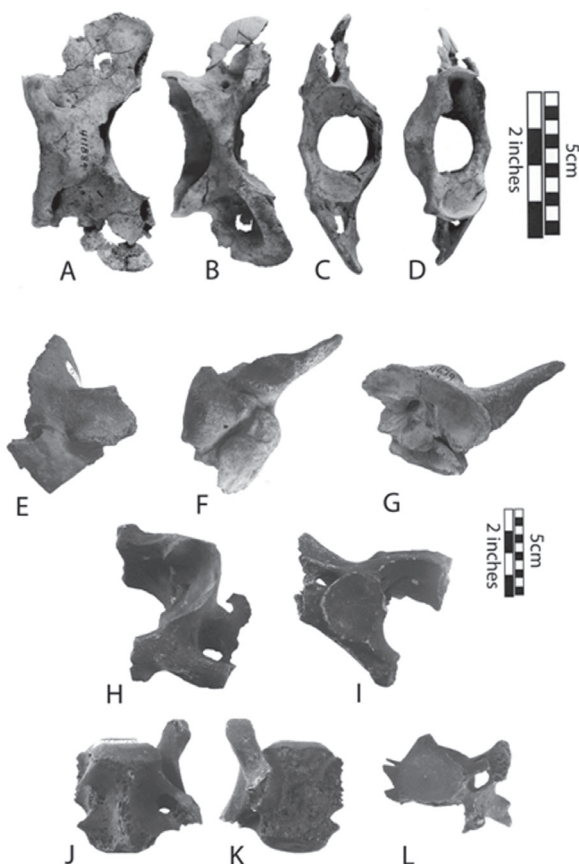


Fig. 4. Atlas and skull. Atlas (C1) of *Leptophoca lenis* from Maryland, USA (USNM 411889) in **A** — dorsal; **B** — ventral; **C** — caudal and **D** — cranial views. Skull fragment of *Terranectes magnus* (CMM-V-4680) in **E** — lateral view; and *T. parvus* (CMM-V-4679) in **F** — lateral and **G**, medial views. Atlas of *T. magnus* (CMM-V-4677) in **H** — cranial and **I** — caudal views. Cervical vertebra of *T. magnus* (CMM-V-4676) in **J**, ventral; **K** — dorsal, and **L** — caudal views.



**Table 1. Measurements of humeri, mm**

Characters	<i>Leptophoca lenis</i>			<i>Terranectes</i>	
	n	M	OR	<i>magnus</i>	<i>parvus</i>
Absolute length	5	122.4	111.0–129.0	–	–
Length of deltoid crest	5	75.6	62.0–82.0	81	–
Height of head	5	25.0	19.5–28.0	32.5	–
Height of trochlea	8	17.6	15.0–19.0	–	28.1
Width of head	5	28.2	22.5–31.0	43.8	–
Width of deltoid crest	2	20.5	17.0–24.0	39.4	35.2
Width of distal epiphysis	9	37.3	35.0–42.0	–	55.9
Width of proximal epiphysis	5	35.7	33.5–38.0	63	–
Width of trochlea distally	9	20.0	18.0–23.0	–	27.2
Width of trochlea, frontal view	8	17.6	15.0–20.0	–	37.2
Transverse width of diaphysis	9	15.9	14.0–17.5	34.0	26.9
Thickness of proximal epiphysis	4	34.8	32.5–38.0	62.2	–
Thickness of medial condyle	10	17.8	15.0–21.0	–	33.3
Thickness of lateral condyle	8	16.8	13.0–20.5	–	20.2
Diameter of diaphysis with deltoid crest	8				

depression between meatal tube and postglenoid foramen.

Humerus: proximal part of deltoid crest located lower than head and lesser tubercle; lesser tubercle oval, flattened; extends higher than head and distal part of deltoid crest; ratio of head's

width to its height is 1.09; deltoid crest strongly developed, short, terminates at middle of diaphysis; greater width of deltoid crest located on its proximal part; deltoid tuberosity hardly noticeable; in lateral view, deltoid crest flattened and oval.

Femur: narrowest width of diaphysis located at middle of bone; condyles relatively large, and placed wide apart; greatest distance between condyles 17.3 mm.

Description — skull, fig. 4, E. Only the glenoid fossa with partial squamosal is preserved. The glenoid fossa measures 20.5 mm anteroposteriorly and 26 mm transversely. Its posterior border is thicker than the anterior and forms a deep postglenoid groove in the tympanic bone. A postglenoid foramen is located at the end of the postglenoid groove. We consider the presence of this foramen to be a primitive condition in Phocidae, in contrast to the opinion of Wyss and Flynn (1993). This foramen is present and large in terrestrial carnivores (Koretsky and Holec, 2002). The postglenoid process itself is located 2 mm in front of the meatal tube. Between the meatal tube and the postglenoid foramen is a shallow, wide depression (in contrast to the groove in *Devinophoca*) in the tympanic bone. This depression is parallel to the meatal tube and floored by the tympanic bone. The suprimeatal fossa is present.

Vertebrae: The vertebral column in Monachinae has the formula C7, T15, L5, S3–4, Ca1–12. The transverse processes on thoracic vertebrae are present from T11 to T15. The

**Table 2. Measurements of ulnae, mm**

Characters	<i>Terranectes</i>	
	<i>magnus</i>	<i>parvus</i>
Width of trochlear notch proximally	15.4	13.5
Width of notch distally	13.9	12.5
Maximal width of middle part of diaphysis	28.7	19.9

**Table 3. Measurements of innominata, mm**

Characters	<i>Leptophoca lenis</i>			<i>Terranectes</i>	
	n	M	OR	<i>magnus</i>	<i>parvus</i>
Length from center of acetabulum to iliac crest	6	73.8	66.0–83.0	64.2	62.2
Width of level of iliac crest	5	59.4	52.0–76.0	71.7	67.8

**Table 4.** Measurements of femora, mm

Characters	<i>Leptophoca</i>						<i>Terranectes</i>	
	<i>lenis</i>			<i>amphiatlantica</i>			<i>mag-nus</i>	<i>par-vus</i>
	n	M	OR	n	M	OR		
Absolute length	2	–	119.0–120.0	2	107.1	96.0–118.3	–	109.4
Medial length	2	–	109.0–112.0	1	109.5	–	–	109.4
Lateral length	6	104.8	101.5–112.0	2	102.0	95.4–109.4	–	98.2
Length of medial condyle	2	–	21.5–22.0	1	19.7	–	–	23
Length of lateral condyle	5	22.9	21.0–24.5	2	19.6	19.4–19.8	31.1	28.3
Length of greater trochanter	4	33.3	28.5–37.0	3	28.8	27.1–30.5	–	37.1
Intertrochanter length	8	44.0	42.0–48.0	3	43.8	38.0–48.8	–	25.1
Height of head	2	–	23.5–25.5	2	18.7	18.3–19.0	–	22.8
Height of articular area of patella surface	6	23.8	23.5–24.0	2	21.5	20.0–23.0	27.8	24.2
Width of proximal epiphysis	8	53.9	51.0–59.0	3	54.8	47.1–59.2	–	58.3
Width of distal epiphysis	4	53.3	54.0–62.0	2	52.4	46.0–58.8	–	64.6
Width of condyles	3	50.7	45.0–54.5	2	47.0	43.0–51.0	–	59.4
Width of greater trochanter	7	18.8	16.5–22.5	3	19.7	18.3–20.5	–	25.2
Width of head	7	20.5	18.0–23.5	2	20.5	18.0–23.0	–	21.5
Width of diaphysis	9	28.1	26.0–35.0	2	27.3	23.7–30.9	45.1	35.9
Anteroposterior thickness of diaphysis	9	15.2	14.0–17.0	3	16.0	15.5–16.5	23.5	22.6
Thickness of medial condyle	3	27.3	27.0–27.5	1	30.0	–	–	18.4
Thickness of lateral condyle	8	28.3	27.0–31.5	2	28.7	26.4–31.0	27.9	22.6
Distance between condyles	8	14.3	13.0–17.5	2	15.1	14.3–15.8	–	11.7
Diameter of neck	9	16.2	14.5–18.0	3	17.7	16.3–18.9	–	22.6

neural spines are high and pointed on the first five vertebrae, but get progressively smaller and more posteriorly inclined.

Cervical vertebrae: figs 4, J–L. The bodies (*centra*) are oval in coronal sections (primitive condition) as in Phocinae, not round as in other Monachinae. The ventral surfaces have a median keel in all except the atlas. The transverse processes are at right angles to the median plane and are directed slightly ventrally, and not divided into two branches as in other Monachinae. Compared with sea lions, the cervical transverse processes of seals are narrower, reflecting less complexity of the *longus colli* muscle. The spinous processes are also less developed.

Atlas: fig. 4, H–I. The atlas (C1) is delicately built, measuring 120 mm in width and 43 mm in dorsoventral height. Its dorsal and ventral tubercles are well marked. The vertebral arch is oval, with a larger anterior radius than posterior. The transverse process is wide; cranially the transverse process is expanded and directed vertically, whereas overall it is inclined caudo-laterally (Koretsky, 2001, table 13). The intervertebral foramen is large, measuring 8.6 mm in diameter caudally, whereas cranially it forms an enormous depression (21.0 mm wide mediolaterally, 17.5 mm anteroposteriorly and 20.3 mm high). The alar notch is not present, in contrast to land carnivores.

Sacrum: fig. 5, D–F. The sacrum consists of 4 fused vertebrae as in other seals (cystophorines and phocines) with an absolute length of 169.5 mm; the greatest width of the wing is 148.0 mm. The sacral promontory is almost flat and not pronounced. However, the ala is thick and the anterior surface of the first centrum is higher than the wings of the sacrum (as in *Mirounga* and monachines, but in contrast to cystophorines and phocines,

**Table 5.** Measurements of tibiae, mm

Characters	<i>Leptophoca lenis</i>			<i>Terranectes</i>	
	n	M	OR	<i>magnus</i>	<i>parvus</i>
Width of proximal epiphysis	16	46.3	44.0–58.0	67.3	50.9
Length of proximal epiphysis	7	28.3	25.0–33.0	44.5	34.7

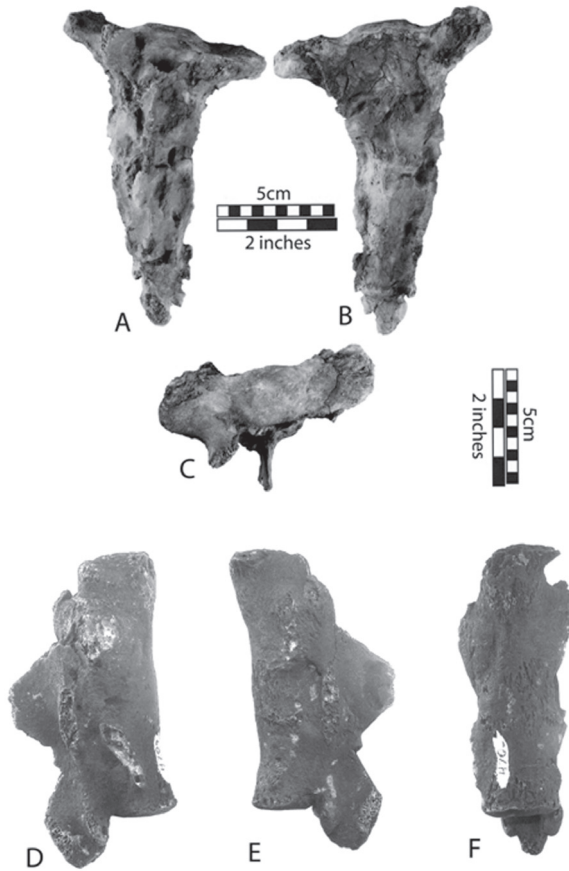


Fig. 5. Sacrum. Sacrum of *Leptophoca lenis* from Maryland, USA (USNM 23231) in **A** — dorsal; **B** — ventral and **C** — cranial views. Sacrum of *Terranectes magnus* (CMM-V-4703) in **D** — lateral; **E** — ventral, and **F** — medial views.

where the ala is on the same level as the centrum; Antoniuk, 1979; Koretsky, 2001). The maximum width across the wings is 87.3 % of the length of the sacrum, which according to Antoniuk (1979) is a monachine character. Thin, slender, and well-defined transverse processes are present on S2. Also on S2 is a well-defined mammillo-articular process (intermediate sacral crest) and a long spinous process that does not extend caudally. S3 shows a shorter spinous process that extends caudally with a less developed mammillo-articular process. The median sacral crest, which is formed by the spinous processes, is not fused. All spinous processes are almost the same size. The body of the sacrum is long and slender.

**Humerus:** fig. 6, D–G; table 1. The proximal part of the deltoid crest is located below the lesser tubercle and the humeral head. The deltoid crest is not strongly developed, relatively short, and very well outlined. The deltoid crest is only slightly wider proximally and terminates abruptly in the middle of the bone. In lateral view, the deltoid crest is visibly flattened and oval in outline. The deltoid tuberosity is hardly noticeable. The lesser tubercle is oval and flattened, extending higher than the head and distal part of the deltoid crest. The intertubercular groove is wide and slightly concave. The head is large and oval, compressed craniocaudally. The musculospiral groove is well expressed.

**Innominate:** figs 7, 8, A, G, I, J; table 3. The ilium is thick and flattened for the insertion of the *gluteus medius* m., which abducts and extends the femur (Piérard, 1971). The iliac crest is slightly averted and not excavated on its ventral surface as in other Monachinae and Cystophorinae (similar to *Terranectes parvus*). The iliopectineal eminence for insertion of the *psaos minor* m. (flexing lumbar vertebral column during caterpillar-like

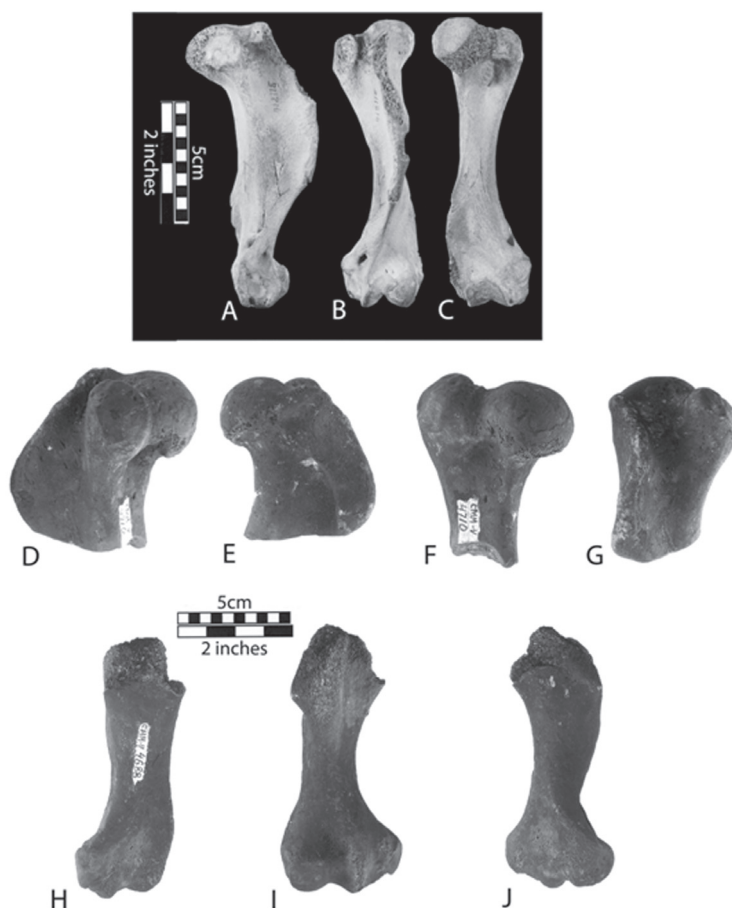


Fig. 6. Humeri. Left humerus of *Leptophoca lenis* from Maryland, USA (USNM 412115) in **A** — medial; **B** — cranial; and **C** — caudal views. Incomplete left humeri of *Terranectes magnus* (holotype, CMM-V-4710) in **D** — medial; **E** — lateral; **F** — caudal and **G** — cranial views; and *T. parvus* (CMM-V-4688) in **H** — medial; **I** — cranial and **J** — caudal views. Scale bars equal 5 cm/2 inches.

terrestrial locomotion; Muizon and Hendey, 1980; Muizon, 1981 c) is wide and very well pronounced (fig. 7, C–D).

The pectineal line is visible. On the ventral side of the ilium, anterior to the iliopectineal eminence, one insertion is present for three muscles (*psaos major* m., *quadratus lumborum* m., and *psaos minor* m.) that aid in flexing the hip joint and rotating the thigh outward (Miller et al., 1964; Muizon, 1981 c). These muscles (*psaos minor* and *major*, and *quadratus lumborum*) work together with the *iliacus* m. to flex the vertebral column in a vertical plane when acting jointly to facilitate locomotion on land. However, when acting alternately they flex the column in a horizontal plane and this movement is used for swimming. The iliac tuberosity (fig. 7, C–D) on the ventral side of the ilium is rounded, large (in contrast to *T. parvus*), and turned anteriorly (for insertion of the *psaos major* and *iliacus* m.).

The *iliacus* m. does not rotate the thigh outward as in other terrestrial mammals (as the *psaos major* m. does not insert on the femur). This is one of the major synapomorphies of phocids (Muizon, 1981, 1981 c; Miller et al., 1964). This tuberosity is generally well-developed in Phocinae and less developed in Monachinae (a primitive character).

The caudal dorsal iliac spine (figs. 7, C–D, 8) is big, thick (similar to *T. parvus*), and has a flattened surface laterally, but is turned medially. On the medial side of the wing is a deep and long auricular fossa for articulation with the sacrum. The edges of the acetabulum are raised slightly above the plane surface (similar to *T. parvus*) of the bone. The acetabulum is

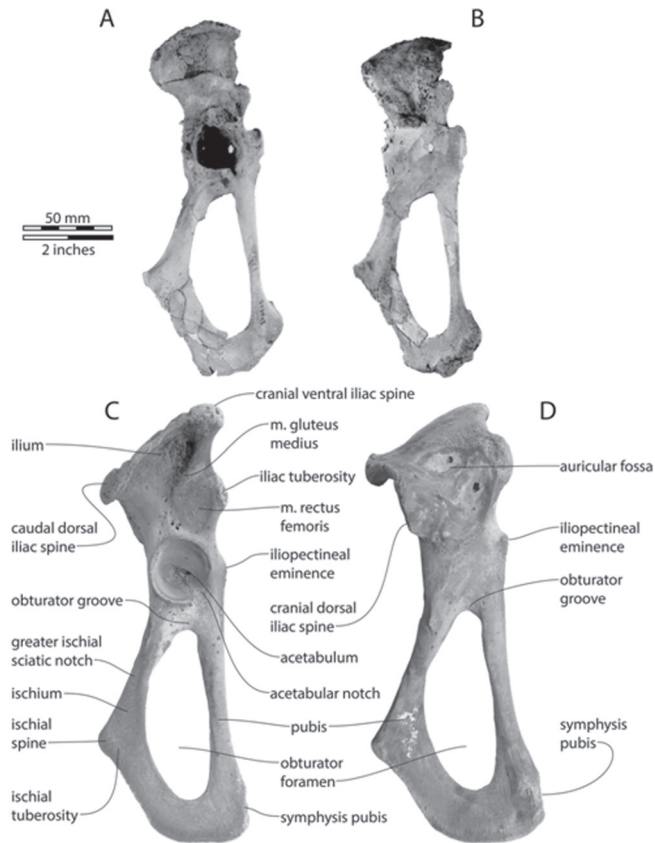


Fig. 7. Modern and fossil innominate bones. Left innominate of *Leptophoca lenis* from Maryland, USA (USNM 263648) in **A** — lateral (reversed) and **B** — medial views. Innominate of Recent *Phoca vitulina* (CMM-O-399, L. and R.) in **C** — lateral and **D** — medial views.

circular, with a deep and well-marked acetabular notch. Anterior to the acetabulum is a big, shallow, and wide depression for the origin of the *rectus femoris* m. (Koretsky and Rahmat, 2013, fig. 8). The incomplete pubis is flattened, and most of the ischium is not preserved.

Femur: fig. 9, E–F; table 4. The minimum width of the diaphysis is located at the midpoint in the length of the bone. The supracondylar fossa, located above the lateral condyle, is shallow and wide. The condyles are relatively big and widely spaced.

Tibia: fig. 10, D–F; table 5. The two condyles are weakly concave on their anterior surface, large, and oval. The intercondyloid eminences are weak and rise only slightly above the lateral borders of the condyles, and especially above the medial border of the medial condyle. The borders of the condyles are well developed. The popliteal notch is shallow and wide, but well-marked. The tibial crest is rounded in a dorsomedial direction. The tibial tuberosity is flattened, well-marked, triangular, and extends along the axis of the bone. The muscular groove is flat and narrow; and the distal end of the bone is missing.

Ulna: fig. 11, A–C; table 2. The medial aspect of the bone is slightly concave. The olecranon is long and slender, sharply connected to the proximal half of the bone. A prominent protuberance of the rugosity for insertion of the *brachialis* m. is present on the medial surface. On the lateral aspect, the fossa for insertion of the *abductor pollicis longus* m. is deep. Caudal to the articular surface on the lateral aspect is a shallow, wide, and long depression. On the bone's radial aspect, the coronoid process noticeably protrudes forward over the radial notch, which is deep and long. On the lateral aspect, the interosseous crest is swollen, forming an oval prominence that protrudes considerably. The head is not preserved.



Fig. 8. Fossil innominata. Innominate bones in lateral view: **A** — *Terranectes magnus* (L., incomplete, CMM-V-4708); **B** — *Terranectes parvus* (L., incomplete, CMM-V-4683); **C** — *Homiphoca capensis* (L., incomplete, South African Museum PQ-L30236; Muizon and Hendey 1980, fig. 12); **D** — *Callophoca obscura* ( $\sigma$ , incomplete, USNM 425886, from Lee Creek Mine, USA; Koretsky and Ray 2008, fig. 33); **E** — *Acrophoca longirostris* (L., incomplete, SAS 563; Muizon 1981a, pl.11, fig. 1); **F** — *Piscophoca pacifica* (R., SAS 682; Muizon 1981a, pl.5, fig.1). In medial view: **G** — *T. magnus* (L., incomplete, CMM-V-4708) and **H** — *T. parvus* (L., incomplete, CMM-V-4683). *T. magnus* (L., incomplete, CMM-V-4708) in **I** — cranial and **J** — caudal views. *T. parvus* (L., incomplete, CMM-V-4683) in **K** — caudal and **L** — cranial views.

## Discussion

According to Muizon (1981 a), *Piscophoca* appears to be very closely related to *Monotherium aberratum* and *Acrophoca* (fig. 8, E). The anatomy of the limb bones indicates a lesser adaptation to swimming than extant Lobodontini and greater adaptation towards terrestrial locomotion. They both are very similar to *Terranectes* (fig. 8, G–K).

The major characters of the innominate bone are: 1) the length of the ilium when compared to most other monachines (except *Monachus monachus* and *Piscophoca*; fig. 8, F); 2) the great development of the iliopectineal eminence; and 3) the position of the cranio-ventral iliac spine, which is anterior to the craniodorsal one. These three characters resemble the phocine condition. But the convex iliac crest, the rounded cranial iliac spines, and the little-everted ilium are typically monachine. In fact, the three major characters mentioned above are plesiomorphic for phocids and, not surprisingly, are also present in phocines.

### *Terranectes parvus* sp. n. (figs 4, 6, 8, 9, 11, 12; tables 1–5)

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Etymology. *Parvus* (Latin, “small”)

Holotype. Femur CMM-V-4709.

Referred specimens. In addition to the holotype, the following specimens were found in southern Virginia near the North Carolina border: Skull fragment: CMM-V-4679; Humeri:

CMM-V-4688, CMM-V-4686 (immature), CMM-V-4687; Ulna: CMM-V-4690 (immature); Innominata: CMM-V-4683, CMM-V-4684; Tibiae: CMM-V-4689 (immature), CMM-V-4778; Fibula: CMM-V-4701; Astragalus: CMM-V-4682; Phalanges (7): CMM-V-4694-4700; Metapodials (3): CMM-V-4691-4693.

Type locality. Site #PQ-BH9812, Southampton County, Virginia near the North Carolina border.

Geological age and distribution. Upper Miocene, Chesapeake Group, Eastover Formation (7.0-6.0 Ma) and St. Marys Formation (10.0-8.0 Ma).

Diagnosis. Seals of medium size.

Humerus: deltoid crest extends about  $\frac{1}{2}$  of bone length (in contrast to *T. magnus*); deltoid tuberosity very pronounced (in contrast to *T. magnus*); in lateral view deltoid crest flattened and oval (similar to *T. magnus*); lateral epicondyle lower and narrower than the medial, does not reach proximal part of deltoid crest; medial epicondyle extending lower than coronoid fossa; coronoid fossa oval and deep.

Femur: proximal part of greater trochanter wider than the distal; trochanteric fossa deep, wide; head small, seated on distinct lip on short and wide neck; supracondylar fossa shallow, narrow, and elongated (similar to *T. magnus*); smallest width of diaphysis shifted proximally (in contrast to *T. magnus*). Innominate iliac tuberosity flattened, small and turned anteriorly; alar spine overhangs.

Description—Skull: fig. 4, F–G. The glenoid fossa measures 16.6 mm anteroposteriorly and 30 mm transversely. Its posterior border forms a very deep, wide postglenoid groove in the tympanic bone. A postglenoid foramen is located at the end of the postglenoid process in this groove, and is not floored by the tympanic bone as in *Devinophoca* (similar to *T. magnus*). The postglenoid process itself is wide (24.8 mm) and is located 7.3 mm anterior to the meatal tube.

Laterally (fig. 4, F–G), the bulla is extended as a long tube, with a prominent ventral lip forming the ventral margin of the round external auditory meatus. The rim of the external auditory meatus is separated by a deep but short notch from the mastoid process (as in other carnivores). As in other phocids (Mitchell and Tedford, 1973), this notch continues as a well-defined groove extending anterolaterally from the stylomastoid foramen along the side of the external auditory meatus. This groove is a synapomorphy of phocids (Koretsky and Holec, 2002). The pit for the tympanohyal ligament is separated from the stylomastoid foramen (a primitive condition) and is anterolateral to the latter (as in *Lontra*; see Muizon, 1982).



Fig. 9. Femora. Femora of *Leptophoca* in dorsal views. *L. amphiatlantica*: A — male, (R., reversed; USNM 23227) from Maryland, USA; B — female, (L., USNM 3211926) from Maryland, USA; C — Male, (L., MAB 2129) from Liessel, southeastern Netherlands; D — *L. lenis* (R., reversed; USNM 263648) from Maryland, USA. Incomplete femur of *Terranectes magnus* (CMM-V-4706) in E — dorsal and F — ventral views. *T. parvus* femur (holotype, CMM-V-4709) in G — dorsal; H — ventral and I — lateral views.



Fig. 10. Tibiae. Right tibia of *Leptophoca lenis* from Maryland, USA (USNM 175578) in **A** — caudal; **B** — cranial; and **C** — proximal views. Incomplete L. tibia of *Terranectes magnus* (CMM-V-4702) in **D** — cranial; **E** — caudal and **F** — proximal views; and incomplete R. *T. parvus* tibia (CMM-V-4778) in **G** — caudal; **H** — cranial and **I** — proximal views.

medial side of the bulla, and the carotid foramen is separated from the posterior lacerate foramen by a thick wall. The carotid canal is partially concealed in the posteromedial wall of the bulla, considerably anterior to the posterior lacerate foramen (primitive conditions according to Tedford, 1977), not reaching the level of the stylomastoid foramen. The posterior opening and the posteromedial process of the carotid canal are visible in ventral view (Ray, 1976). In *T. parvus* (similar to *L. lenis*, but in contrast to *D. claytoni*) the carotid canal is parallel to the surface of the basioccipital, but in contrast to *D. claytoni* its posterior aperture opens in a ventral direction (derived condition, as in other phocines), and has a fully formed margin at its medial side (this is the primitive condition).

The posterior lacerate foramen is impossible to describe because the basioccipital bone is partially broken. However, the septum between the carotid canal and the posterior lacerate foramen is present (in contrast to ursids, otariids, and primitive musteloids; Mitchell and Tedford, 1973; Tedford, 1977; Wolsan, 1993).

The mastoid process is wide, extends far laterally (as in Monachinae), and forms a pronounced prominence anterolateral to the auditory bulla. The mastoid is so inflated that it is almost the same height as the bulla in lateral view. There is a complete fusion of the posterolateral portion of the meatal lip to the mastoid process as in other carnivores, but the deep groove is present anteromedially. The continuous crest extending from the mastoid process over the external auditory meatus to the postglenoid process is very well developed.

In ventral view (fig. 4, F–G), the tympanic bulla is roughly triangular in outline, has a smoothly convex ventral surface, is slightly inflated in its anterior (= ectotympanic) parts, and slopes uniformly to the posterolateral parts. The length of the auditory bulla (40.2 mm) is 2.4 times the anteroposterior width of the glenoid fossa, as in other monachines, but in contrast to *Devinophoca* (3.4 times). The long axis of the bulla is parallel to the midline of the skull. The median lacerate foramen and musculotubular canal with the petrotympanic fissure (= groove) are separated by a thin septum (3.0 mm) above the anteromedial corner of the bulla. The inflated ectotympanic part is bigger than the entotympanic (in contrast to *D. claytoni*). Caudally, the entotympanic is more flattened than the ectotympanic along the anteroposterior axis, and is separated from the ectotympanic part of the bulla by a distinct ridge instead of a sulcus. This flatter entotympanic is in contrast to the more inflated entotympanic of Mustelinae and other Phocidae, as noted by Wozencraft (1989).

The medial portion of the entotympanic close to the petrosal bone forms a deep, long fissure around the



Humerus: fig. 6, H–J; table 1. The deltoid crest extends about half the length of the bone, and smoothly descends to the condyles as a flat, almost invisible ridge. The deltoid tuberosity is large and located at the distal end of the deltoid crest. The lateral epicondyle is longer and narrower than the medial, and does not reach the distal part of the deltoid crest. The medial epicondyle is flattened, extending lower than the coronoid fossa. The entepicondylar foramen is absent. The coronoid fossa is deep, oval, extends further proximally than the lateral epicondyle, and ends at the same level as the medial epicondyle. The olecranon fossa is very shallow.

Innominate: figs 7, 8, B, H, K, L; table 3. As in other Monachinae and Cystophorinae, the ilium is thick and the iliac crest is not everted and not excavated on its ventral surface. The iliopectineal eminence is well pronounced (as in *T. magnus*), and situated higher than the proximal border of the acetabular fossa.

The iliac tuberosity is flattened, small and turned anteriorly (in contrast to *T. magnus*). The greater ischial notch is slightly concave, almost straight. A shallow depression (fossa) for the *gluteus medius* m. is located on the lateral aspect of the ilial wing. The alar spine protrudes very far. The edges of the acetabular fossa are raised above the plane surface of the bone. The acetabulum is circular with a deeply marked cotyloid notch. The ischium is flattened, wide and thin. The ischial spine is small, elongated and well developed for attachment of the *biceps femoris* m. The pubis is not preserved.

Femur: fig. 9, G–I; table 4. The greater trochanter extends proximally slightly higher than the head; its proximal part is wider than the distal. The trochanteric fossa is deep, wide, and opens distally, reaching the distal border of the head. The flat and wide intertrochanteric line disappears at the middle of the diaphysis, which serves for insertion of the *iliopsoas* m. The femoral head is small, relative to the bone's mass, and is seated on a very short and thick neck. Between the head and neck is a distinct lip. The smallest width of the diaphysis is shifted toward the proximal end of the bone. The supracondylar fossa is located above the lateral condyle and is shallow, narrow, and elongated. The condyles are unequal in size.

Tibia: fig. 10, G–I; table 5. The two condyles are strongly concave in their centers, shortened, small, and oval. The intercondyloid eminences are large and rise above the two lateral, weak borders of the condyles. The popliteal notch is deep, wide, and well-marked. The tibial crest is rounded in a dorsomedial direction. On the ventral side of the tibia, the tibial tuberosity is flattened and well-marked.

Ulna: fig. 11, D–F; table 2. The medial surface of the bone is concave. The olecranon is short and thin, gradually connecting to the proximal half of the bone. On the lateral surface, is a very visible prominence of the rugosity for insertion of the *brachialis* m. A protuberance is present for origin of the *abductor pollicis longus* m. A sharp crest is located caudal to the articular surface. On the bone's radial aspect, the coronoid process protrudes only slightly forward over the radial notch, which is deep and wide. The interosseous crest is sharp, forming a prominence. The head is not preserved.

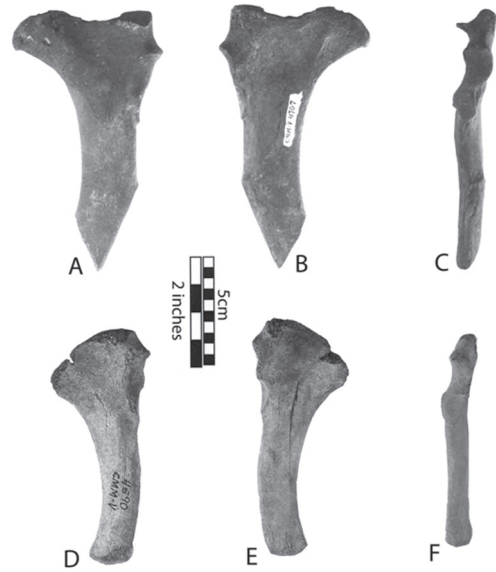


Fig. 11. Ulnae. Incomplete L. ulna of *Terranectes magnus* (CMM-V-4707) in **A** — lateral; **B** — medial and **C** — cranial views. Incomplete L. immature ulna of *T. parvus* (CMM-V-4690) in **D** — lateral; **E** — medial and **F** — cranial views. Scale bar equals 5 cm / 2 inches.

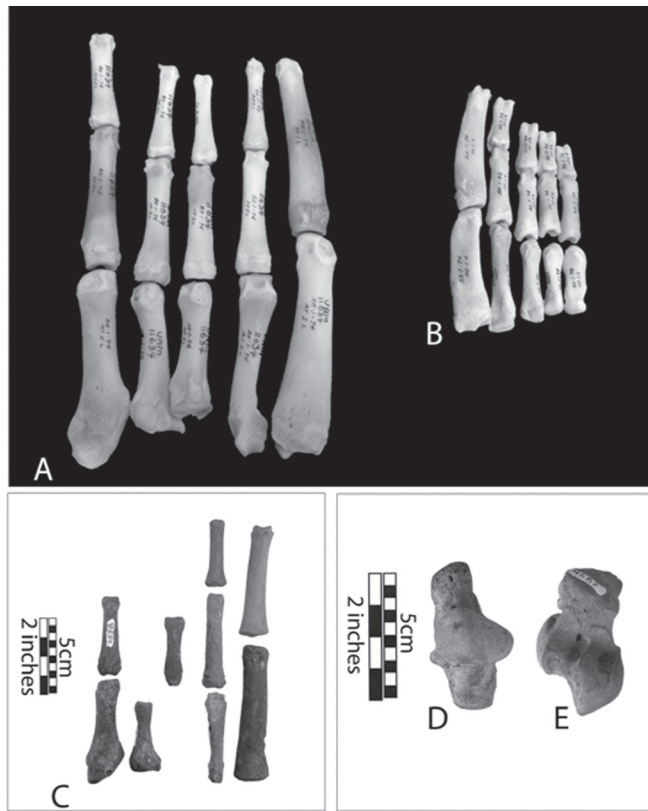


Fig. 12. Pes. Phalanges of Recent spotted seal (*Phoca largha*; UAM 11634) in **A** — hindfoot and **B** — forefoot. **C** — incomplete, reconstructed left hindfoot of *Terranectes parvus* (CMM-V-4691-4700). Metatarsal bones found separate and placement of some phalanges uncertain. Astragalus of *T. parvus* (CMM-V-4682) in **D** — cranial and **E** — lateral views.

## Discussion

The classification of fossil seals using mainly postcranial elements has been questioned frequently by non-seal specialists. As we mentioned several times in previous publications (Koretsky and Rahmat, 2013; Koretsky et al., 2014), due to the rarity of cranial remains, the study of fossil seals has been based mainly on postcranial features, specifically the morphology of individual dissociated bones (mainly the femur or humerus). The paper-thin thickness of seal skull bones makes it even more difficult to find cranial fossil material (presently, only 15 fossil seal skulls have ever been found and described worldwide; Koretsky and Rahmat, 2013). Analysis of morphological characters relating to ecomorphotypes of extant seals can be used to interpret postcranial characters (Koretsky, 2001). This has allowed separation of modern and fossil seals into ecomorphological groups based on characters from the most common dissociated elements. In addition, other publications show associated parts of seal skeletons (Muizon, 1981 a; Cozzuol, 2001; Koretsky, 2001; Koretsky and Grigorescu, 2002; Koretsky and Ray, 2008; Koretsky and Rahmat, 2013) that also can be used as a foundation for alpha classification. Distinctive morphological variation provides the basis on which individual bones from the Upper Miocene Chesapeake Group were divided into two taxonomic groups.

After analyzing two size clusters of specimens (36 individual fossil cranial and postcranial bones) from the western shore of the Chesapeake Bay, it was determined that they did not fit known patterns of ontogenetic (both clusters have fused epicondyles) or sexual variation. As discussed by Koretsky (2001), the following characters can be used for

sexual determination: 1) on the humerus — depth of fossa for the *triceps medialis* muscle; overall size; length of deltoid crest and width of its middle part; depth and shape of the coronoid fossa; depth of fossa located caudal to medial side of neck of the humerus, distal to lesser tubercle; and 2) on the femur — degree of compression of the femoral shaft; overall size; anteroposterior width, or dorsoventral thickness of diaphysis; length and thickness of neck; length and width of greater trochanter; anteroposterior diameter of distal epiphysis. In addition, most elements of the postcranial skeleton for both new species reveal several very primitive characters, such as presence of a visible femoral intertrochanteric line and a large, deep acetabulum. This generally primitive aspect of the bones supports the taxonomic homogeneity of these dissociated remains.

## Conclusion

The paleontological record confirms biogeographical, phylogenetic, and morphological arguments indicating separate ancestries for phocids and otarioids, with phocids originating in the North Atlantic and otarioids in the North Pacific (Koretsky and Barnes, 2006). The recently described *Afrophoca libyca* (Koretsky and Domning, 2014), the oldest seal known from the Eastern Hemisphere, also supports the hypothesis that Phocidae originated in the Paratethyan and / or Mediterranean Basins no later than the Late Oligocene. Geologically younger Miocene seals were not very similar morphologically to any known terrestrial or semiaquatic carnivorans that could have been the original ancestors of phocids. They also did not differ very much from modern species. Structure of the dentition, cranium, and postcranial skeleton, as well as the relatively early geological ages of these seals, support the conclusion that these Oligocene–Neogene taxa include the ancestors of some extant Phocidae.

Both newly collected and previously well-known (from different museum collections) material from the eastern shore of the North Atlantic, studied in relation to fossil seals from the western shore, sheds new light on distribution of true seals in the North Atlantic (Ray, 1976, 1977; Repenning et al., 1979; Ärnason, 2006; Koretsky and Barnes, 2006; Koretsky et al., 2012; Koretsky and Rahmat, 2013). Their ranges in the North Atlantic Ocean evidently expanded to occupy all suitable and accessible habitats. Many of these Miocene and Pliocene seals were distributed more or less continuously around the northern perimeter of the North Atlantic.

There are two distinct categories of seals known from the Calvert and St. Marys Formations (Ray, 1976; Koretsky, 2006; Koretsky et al., 2012), indicating a well-marked divergence between phocines and monachines earlier than 18 million years ago, as previously thought. The monachine seal *Monotherium? wymani* from the Calvert Formation (according to Ray, 1976), from Richmond, Virginia, USA, and also the phocine seal *Leptophoca lenis* (St. Marys Formation) had unquestionably diverged already from a common ancestor when they settled along the western shore of the Atlantic. This is supported by the current molecular data that estimate the time of separation between Monachinae and Phocinae at ~22 Ma (Ärnason et al., 2006), considerably older than the ~15–17 Ma suggested by Fyler et al. (2005).

In the Miocene (23.0–5.0 Ma) deposits of the Chesapeake Group, only two subfamilies of the Family Phocidae were identified: Phocinae and Monachinae. *Leptophoca*, a small-sized phocine, is present on both sides of the Atlantic Ocean, in The Netherlands and Maryland and Virginia (USA). *Leptophoca amphiatlantica* originated on the shore of Western Europe (Holland, 16.4–15.8 Ma), crossed the Atlantic westward, and settled on the western shore of the North Atlantic, first in Calvert time (15.0–14.2 Ma) and later spreading southward in St. Marys time (10.5–8.5 Ma). The newly described monachine seals, *Terranectes* spp., appeared on the eastern shore of North America, first in the St. Marys Formation (10.0–8.0 Ma) and later in the Eastover Formation (7.0–6.0 Ma).

The Miocene fossil seals from Calvert Cliffs (USA) represent a limited taxonomical range of Phocidae compared with the geologically later fauna in the Lee Creek Phosphate Mine of North Carolina (Pliocene) and younger faunas from the Black Sea region of the Paratethys (Eastern Europe) from the Early Miocene. As of now, six seal genera of two subfamilies have been described from the Lee Creek Mine, whereas only two genera from two subfamilies are known from Calvert Cliffs. Future phocid studies require finding and describing more fossil material from Calvert Cliffs to correlate with the taxonomic diversity present in the Yorktown Formation of the Lee Creek Mine. Ideally, associated parts of the skeleton, including cranial (i. e. skull, mandible) and postcranial elements, would need to be found to fully determine taxonomic relationships, nomenclature, and ecological and biogeographical interpretations of fossil seals, as has been done for *L. lenis*.

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